Fast saccadic and manual responses to faces presented to the koniocellular visual pathway

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The parallel pathways of the human visual system differ in their tuning to luminance, color, and spatial frequency. These attunements recently have been shown to propagate to differential processing of higher-order stimuli, facial threat cues, in the magnocellular (M) and parvocellular (P) pathways, with greater sensitivity to clear and ambiguous threat, respectively. The role of the third, koniocellular (K) pathway in facial threat processing, however, remains unknown. To address this gap in knowledge, we briefly presented peripheral face stimuli psychophysically biased towards M, P, or K pathways. Observers were instructed to report via a key-press whether the face was angry or neutral while their eye movements and manual responses were recorded. We found that short-latency saccades were made more frequently to faces presented in the K channel than to P or M channels. Saccade latencies were not significantly modulated by expressive and identity cues. In contrast, manual response latencies and accuracy were modulated by both pathway biasing and by interactions of facial expression with facial masculinity, such that angry male faces elicited the fastest, and angry female faces, the least accurate, responses. We conclude that face stimuli can evoke fast saccadic and manual responses when projected to the K pathway.

Introduction

Faces are some of the most important stimuli for humans, conveying the state, status, and intentions of others. Because of this, visual attention toward, and perception of, faces are of great interest in the study of the human brain and behavior. Faces at a typical viewing distance are too large to fit within the fovea (approximately 2°) and tend to first appear in the visual periphery. Therefore, the most informative parts of the face, such as the eye and mouth regions, have to be identified with peripheral or parafoveal vision, and then the fovea must be positioned on these regions via eye movements. Given that visual processing proceeds along several parallel channels, the magnocellular (M), parvocellular (P), and koniocellular (K) pathways, with different spatial, chromatic, and temporal properties, it is surprising that the contributions of the three major visual pathways affective face perception are only now beginning to be unraveled.

Recently, we have demonstrated that two of the major visual pathways, the M and P pathways, are attuned to somewhat different aspects of face perception (Adams et al., 2019; Cushing et al., 2019; Im et al., 2018; Im et al., 2017). The M pathway, which is formed from the large retinal ganglion cells that combine the inputs of long (L) and medium (M) wavelength cones (i.e., $L + M$) and some rod contributions, is largely insensitive to color but has high gain and sensitivity to small

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luminance differences (Merigan & Maunsell, 1990). It can resolve low and middle spatial frequencies and high temporal frequencies. We have found the M pathway to be more engaged by clear threat cues conveyed by congruent facial expression and eye gaze (Cushing et al., 2019; Im et al., 2017; Im et al., 2018) and clear threat in visual scenes (Kveraga, 2014). The P pathway, formed from the midget retinal ganglion cells that combine the inputs of L and M cones in color-opponent fashion (i.e., $L–M$), is sensitive to color in the green-to-red range, and can resolve higher spatial and low temporal frequencies. We found it to be more attuned to incongruent threat cue combinations of facial expression and eye gaze (Cushing et al., in press; Im et al., 2017; Im et al., 2018). The third, K pathway, formed from the tiny, speck-like retinal ganglion cells that combine the inputs of short-wavelength sensitive (S) cones with the combined inputs of long and medium wavelength cones (i.e., $S - [L+M]$), has received less attention than the M and P pathways until relatively recently (Casagrande, 1994; Hendry & Reid, 2000). Given that the K pathway is a phylogenetically older pathway that serves as the opponent color channel in mammals with dichromatic vision (which comprise the majority of mammals; e.g., Peichl, 2005), it would be reasonable to expect it to also be attuned to identification of biologically relevant stimuli, particularly ones displaying threat cues. Whether saccades to threat stimuli are triggered via K inputs, and what threat cues the K pathway might be attuned to in humans, is unknown. Recent evidence from studies by Hall and Colby (Hall & Colby, 2013; Hall & Colby, 2014; Hall & Colby, 2016) in macaque monkeys with simple dot stimuli showed that neurons in the macaque SC respond strongly to short-wavelength (violet-blue) light with proper calibration of K-biased stimuli. Whether fast saccadic responses could be triggered by more complex stimuli, such as faces, projected to the K pathway, and whether these responses would be modulated by threat cues in the faces, is unknown.

Therefore, the major goals of our study were to test 1) whether biological threat stimuli, human faces, could evoke fast gaze orienting responses when presented to the K pathway and 2) whether saccadic and manual responses would be modulated by facial threat cues. Given its putative role in threat detection (Isbell, 2006; Van Le et al., 2013), we predicted that stimuli presented to the K pathway would evoke faster saccadic and manual responses, compared to stimuli presented to the M or P pathways. The threat cues present in faces can be dynamic and fleeting, such as anger or fear expressions that respectively signal danger to the observer and the expresser, with the threat locus indicated by overt attention cues such as eye gaze direction (Adams et al., 2003; Adams & Kleck, 2003; Adams & Kleck, 2005; Adams et al., 2012; Cushing et al., 2018; Cushing et al., 2019; Im et al., 2017; Im et al., 2018). Facial threat cues also can be more stable or static, inherent in the facial configuration and texture associated with higher masculinity, such as a low, pronounced brow ridge, small eyes, a prominent jaw, facial hair, and a high facial width-to-height ratio (Zebrowitz & Collins, 1997; Zebrowitz & Montepare, 2008). It has been argued that facial expressive cues have evolved to mimic (and amplify) stable configural cues (Adams et al., 2010; Adams et al., 2017; Becker et al., 2007; Marsh et al., 2005). Specifically, it has been found in numerous studies now that anger displayed on male and highly masculine faces is perceived to be more intense, and is recognized more quickly and accurately than angry female or highly feminine faces (see Adams et al., 2015 for review).

To test these hypotheses, we designed a task in which human observers viewed neutral or angry faces that were male or female and varied in masculinity across the stimulus set. The face stimuli were individually calibrated (see Methods) for each observer so as to bias processing towards the M, P, or K pathways, using procedures previously used in (Anstis & Cavanagh, 1983; Cushing et al., 2019; Im et al., 2017; Im et al., 2018; Kveraga, 2014; Kveraga et al., 2007; Thomas et al. 2012) and were briefly presented to the left or right of the central fixation cross. We instructed observers to fixate in the center at the start of a trial, and then to categorize the face as angry or neutral, reporting their decision with a key press as quickly and accurately as possible. Observers were not instructed to make a saccade to the stimulus (or to any other location) and were told that they could look wherever they found to be most helpful to respond most efficiently by key press. The reason for such instructions was that we wanted to observe eye movement patterns evoked by the different types of stimuli, rather than requiring observers to make saccades to all target stimuli as quickly as possible. We tracked the observers' eye movements to test our hypotheses that faces presented to the K pathway 1) would evoke fast saccades and manual responses to the stimulus; and 2) that the response pattern would be modulated by the threat cues conveyed by the stimulus faces.

Methods

Participants

We recruited 33 participants. Of these, the eyes of 30 subjects (21 women and 9 men) could be reliably tracked by our Tobii T120 Dual Eyetracker. All subjects were screened for normal or corrected-to-normal visual acuity, color perception, and contrast sensitivity via pretests described below and provided their informed consent to participate via an Massachusetts General

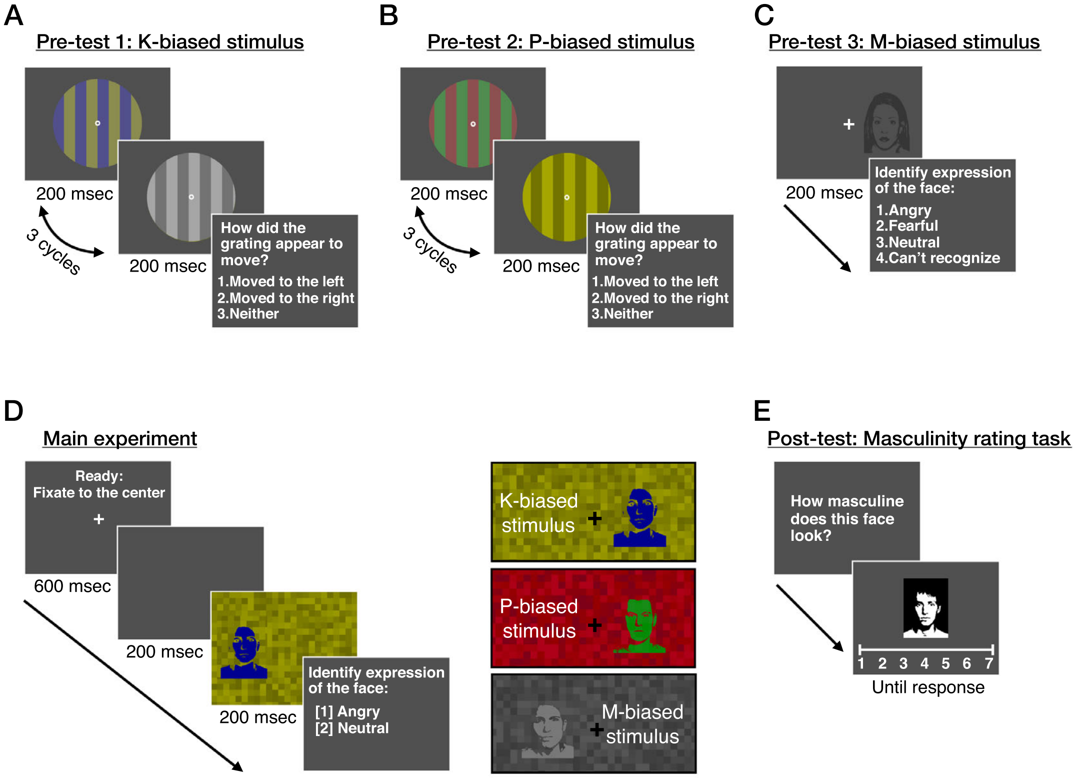

Figure 1. Experimental procedures. (A) Pre-test calibration procedures for the koniocellular-biased stimuli, (B) parvocellular-biased stimuli, and (C) magnocellular-biased stimuli. (D) The trial sequence in the main experiment and examples of K, P, and M stimuli. E. The post-test rating task.

Hospital (MGH) consent form. The study was approved by the MGH Institutional Review Board under protocol #P001227.

Stimuli and procedure

Calibration tests(Figure 1A–C): Before commencing the experiment proper, we determined the luminance contrast threshold, the red-green isoluminance values, and the blue-yellow isoluminance values for each observer via the following procedures. Pretests 1 and 2 (luminance contrast thresholds for K-biased and P-biased stimuli): Figure 1A,B illustrate sample trials of pretests 1 and 2. For both pretests, the chromatically defined, isoluminant stimuli was customized to each participant's isoluminance point. To find the color isoluminance values for K-biased (yellow and blue) and for P-biased (red and green), we used the minimum motion technique (Anstis & Cavanagh, 1983). Briefly, this method uses two interleaved square-wave gratings (e.g., red-green and dark yellow-light yellow) displaced by a quarter cycle to generate apparent motion. According to the minimum motion technique (Anstis & Cavanagh, 1983), when red-green grating is followed by the dark yellow-light yellow grating, a darker color bar—between red and green—will appear to jump to the side of the dark yellow. When the red and green bars become equiluminant, however, then no consistent apparent motion would be perceived. We used large circular gratings encompassing both of the stimulus locations for 40 trials to establish red-green and blue-yellow isoluminance values for each observer. On each trial, 6 gratings were presented in a sequence, each of which lasted for 200 msec. Each grating was displaced sideways by half a bar width from its predecessor. Because direction of apparent motion depended on the perceived luminance of the bars, we asked participants to make a key press to indicate which direction either to the left or to the right the grating appeared to move. The initial red, green, and blue (RGB) values of the yellow, blue, red, and green were (130 130 0), (0 0 130), (130 0 0), and (0 130 0), respectively, then blue and green values were adjusted based on participants' responses to determine perceptual isoluminant points on a participant-by-participant basis.

Pretest 3 (luminance contrast threshold for M-biased stimuli): The luminance contrast sensitivity pretest used a double-staircase procedure in which face stimuli were displayed at varying grayscale values, including catch trials (25%) whose grayscale value was the same as the background value, similar to the procedure used in (Cushing et al., 2019; Im et al., 2017; Im et al., 2018;

Kveraga et al., 2007; Thomas et al., 2012). Figure 1C illustrates a sample trial of pretest 3. Participants were presented with a grayscale stimulus image for 500 msec and instructed to make a key press to indicate the facial expression (neutral, fearful, or angry), or to report being unable to identify the stimulus. To find the threshold for foreground-background luminance contrast, our algorithm computed the mean of the turnaround points above and below the gray background (80 80 80 RGB value on the 8-bit scale of 0–255). From this threshold, the appropriate luminance (approximately 3.5% Weber contrast) value was computed for the face images to be used in the low-luminance-contrast (M-biased) condition.

Main experiment (Figure 1D): For the experiment proper, we selected a new set comprising 44 face stimuli from the FACES data sets (Ebner et al., 2010). The faces of the same individuals displaying a neutral and an angry expression were used in the study. Male and female faces were used, with a 50/50 split, to test the influence of identity cues. The face stimuli were first converted to two-tone images via a thresholding procedure, as in Im et al. (Im et al., 2017), and then individually tailored values obtained from the pretests conducted for each subject immediately preceding the experiment were applied to the stimuli to be shown in the M-, P-, and K-biased conditions. Following the approach by Hall & Colby (Hall & Colby, 2013; Hall & Colby, 2014; Hall & Colby, 2016), the face stimuli were displayed on a dynamic equal-energy gray (EEG) background, comprising 1.2° squares with grayscale values ranging between 72 and 88 (in a range of 0 to 255), which changed every 4 monitor frames (approximately 67 msec). Displaying stimuli on an EEG background masks the contributions of any remaining small luminance differences so that only chromatic information (in the K and P conditions) is useful in perceiving the stimulus. In the M condition, we employed the same EEG background for consistency, with the idea that larger luminance difference between stimulus foreground and background be used to perceive the stimulus.

At the start of the experiment proper, subjects were positioned in a chin-and-forehead rest approximately 60 cm from the eye-tracker display, and seating height was adjusted if necessary to ensure participant comfort. The observers' eye gaze position with respect to calibration points presented on the Tobii T120 17" TFT monitor with integrated binocular eye-tracker was calibrated via a 9-point matrix calibration procedure (iMotions Inc.). The sampling rate of the eye-tracker was set at 120 Hz. If the calibration was unsatisfactory, it was repeated until good calibration was achieved, or it was determined that good calibration was not achievable with that subject, in which case the experiment was terminated.

After the calibration, subjects performed 24 practice trials (8 trials per block) to acquaint themselves with the experimental procedure. Subjects were instructed to report whether the face stimulus, presented in M-, P-, or K-biased forms, displayed an angry or a neutral expression via a key press. The index and middle fingers were to be used for angry/neutral decisions, using the keys {"J" and "K"}. The key assignments for each emotional expression were counterbalanced across subjects. A central fixation cross was displayed for 600 msec at the start of each trial. Observers were instructed to fixate the cross, but could shift their gaze as they wished to make the angry/neutral manual response decision as quickly and accurately as possible. After the fixation cross was removed, there was a gap of 200 msec before the face stimulus (size of 4.74° × 6.32°) appeared for 160 msec, centered at 6.55° left or right of the fixation cross. The gap was used as it is known to elicit short-latency, express saccades with suitable stimuli (Reuter-Lorenz et al., 1991). The stimulus duration was kept short (160 msec) to minimize exploration of the stimulus via saccades and to encourage fast saccades to the stimulus.

Faces in the M, P, and K conditions were presented on the Tobii T120 17" TFT Display/Eye-Tracker set to maximal brightness. The stimuli were presented in blocks of 176 trials, with the block sequence following in pseudo-random order. In the K blocks, the background between trials was set to yellow field (with the R and G values set to 130 on the 0−255 8-bit scale, and the luminance values of 65.58 cd/m^2) to induce adaptation, which in addition to our other manipulations was designed to maximize responses from S-cone inputs (Hall & Colby, 2013; Smithson, 2014). The adjusted B value for the blue foreground resulting from the pretest 2 was 173.95 on the 0−255 8-bit scale on average (luminance values of 13.43 cd/m^2). In the P blocks, the background was set to red (with the R value of 130, luminance value of 19.87 cd/m^2) to suppress M-cell activity (Hall & Colby, 2013; Smithson, 2014). The adjusted G value for the green foreground resulting from the pretest 3 was 155, with the luminance value of 81.89 cd/m^2 on average. In the M blocks, the background was gray with RGB value of (80 80 80), with the luminance value of 36.78 cd/m^2, while the adjusted foreground values from the pretest 1 had a mean of 76.14 (luminance values = 34.89 cd/m^2) on average.

After the main experiment, subjects were asked to conduct a post-test rating task (Figure 1E) in which the face stimuli (angry and neutral) appeared as two-tone black-and-white stimuli for unlimited viewing. The task was to rate on a Likert scale (range of 1−7) how masculine each face appeared. The ratings were collected to examine how facial masculinity cues influence perception of facial expression, and whether

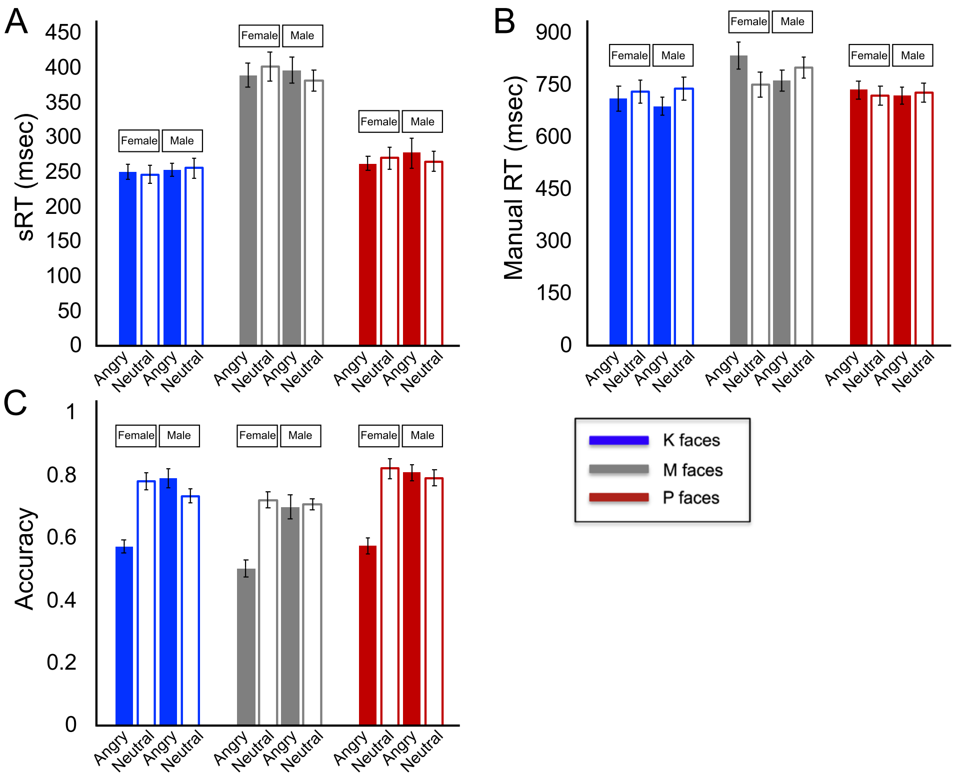

Figure 2. Overall measured variables. (A) Average latency of initial saccades. (B) Average manual response times. (C) Average accuracy of manual responses.

these compound expressive and identity cues interact with the visual pathway to which the face stimuli are presented.

Results

Saccade latencies

We conducted a 3 (*Bias*: M | P | K) × 2 (*Expression*: Angry | Neutral) x 2 (*Identity*: Male | Female) repeated-measures ANOVA to examine the main of effects and interactions by these factors on our measures of variables. The measured variables we examined in depth were: 1) latency of initial saccade [sRT]; 2) accuracy of initial saccade [sAcc]; 3) manual key-press response latency [mRT]; and 4) manual accuracy [mAcc]. The measures of the latency and accuracy of the saccadic eye movements were calculated by using the LandRate toolbox (Krassanakis et al., 2018). In addition, to ensure that the visual pathway biasing did not affect the initial central fixation (required for a trial to be included in the analysis), we assessed the rates of prestimulus fixation for M, P, and K conditions. We found high fixation compliance and no differences between the pathway conditions $F(2,87) = 0.025$, $P > 0.975$. Because the sRT latencies were not normally distributed, but rather were positively skewed, as is typical for response latency distributions (Luce, 1986; Ratcliff, 1993; Van Zandt, 2002), we used the median latencies. We only included sRTs that were followed by correct manual responses in these analyses, as the processes leading to incorrect response can be varied and more variable (however, tables of descriptive statistics, statistical effects, and figures for all trials are included in Supplementary Information). Repeated-measures within-subjects ANOVA of the median sRT revealed a significant main effect of bias $F(2,54) = 73.2$, $P < 0.001$, but no significant main effects of *Expression* or *Identity*, nor any significant interactions (all *P*s > 0.39, tables reporting the results of all statistical tests are included in Supplementary Information). The significant main effect of bias was the result of sRTs being much shorter for K-biased (approximately 251.68 msec) and P-biased (approximately 269.06 msec) stimuli than for M-biased (approximately 392.65 msec) stimuli (Figure 2A). Of these saccadic responses, 7.3% of the total trials evoked express/short-latency saccades (<180 msec) in the K-biased block, versus 2.9% and 5.92% of the trials evoking such saccades (<180 msec) in the M-biased and P-biased blocks, respectively. To investigate these differences in short-latency saccades between the pathway-biasing conditions further, we

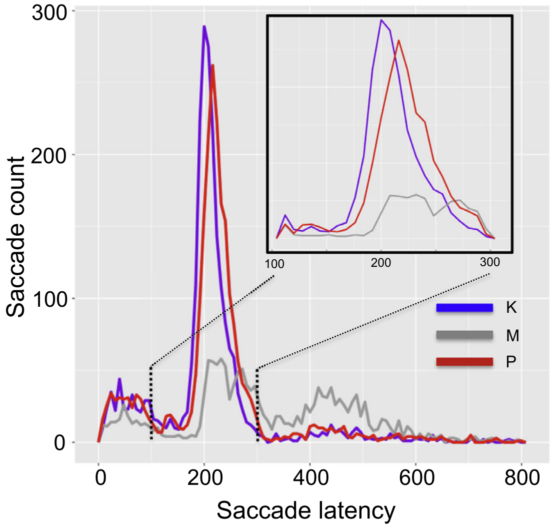

Figure 3. Latencies of initial saccades for M, P, and K stimuli. Distributions of the initial saccadic latencies for correct responses in the range of 0-800 msec. The inset in the top right shows a zoomed-in view of the distributions in the time period of 100—300 ms.

performed a more detailed analysis of saccadic latency distributions.

Response latencies are not normally distributed but typically can be described as the summation Gaussian and exponential distributions (Van Zandt, 2002). However, this can vary depending on the task and modality, and examining response distributions, rather than just looking at the measures of central tendencies (such as the mean or median) more closely can reveal much more information about response tendencies in particular conditions. Figure 3 shows the distributions of the saccade latency for the K-, M-, and P-biased stimuli, which reveal that saccades to faces presented in the K channel had shorter latencies than saccades presented to faces in the P or M channels. We confirmed that these distributions were statistically different from one another by using Kolmogorov-Smirnov tests for all comparisons (K vs. M, P vs. M, and K vs. P; all *P*s < 0.001), with the mode of the distribution being earlier for saccades to K faces (approximately 200 msec) than those to P (approximately 220 msec) or M faces (multiple modes).

Saccade accuracy

Analysis of the initial saccade accuracy (sAcc) revealed different patterns of K, P, and M conditions. Accuracy was defined as the end point of the first saccade landing on the stimulus location, as opposed to being in the central 5.22° × 5.22° area, or opposite the stimulus location (i.e., an antisaccade made in error). Recall that face stimuli appeared in 15 Hz luminance noise briefly (160 msec), and were either isoluminant (K or P) or had a small luminance contrast (M). For the K and P conditions, the majority or plurality (50.8% of K and 49.4% of P) of initial fixation saccade locations landed on stimulus, whereas only 36.8% of M trials evoked an initial saccade to the stimulus. The rest of the initial saccades were in the central 5.22 °× 5.22 °area. This suggests a qualitatively different pattern of response to M stimuli whereby observers often made their response decision without attempting to foveate the stimulus face.

Manual response latencies

The manual latency differences between the K (733.28 msec), P (738.5 msec), and M (789.2 msec) conditions were far less dramatic than sRT latency differences (Figure 2B). There was a significant main effect of bias $F(2,54) = 6.28$; $P < 0.01$. Although main effects of expression and identity were not significant (Ps > 0.381), the interaction between them was $F(1,27) = 22.77$; $P < 0.001$. This was driven by the expected amplification or attenuation of emotional facial expression by the expresser's sex-linked facial identity cues (Adams et al., 2017; Adams & Kveraga, 2015) with angry male faces evoking faster more accurate responses, and angry female faces producing slower and less accurate responses, than the overall mean. A *Bias* * *Expression* * *Identity* interaction suggested $F(2,54) = 2.73$; $P = 0.075$ a trend, but post hoc tests showed that this interaction was mainly driven by M-biased results (Expression * Identity interaction $F(1,27) = 22.24$; $P < 0.001$), whereas K and P showed no significant interactions. These results suggest that when there is more uncertainty about the expression (as when perceptual conditions are difficult, as they seemed to be in the M condition), observers may rely more on other cues (i.e., face identity) for their response decisions (Kveraga et al., in press). This implies that the identity cues (facial masculinity or femininity) are easier to perceive than facial expressions, which, it has been argued, are inherently ambiguous and benefit from contextual cues (Aviezer et al., 2017).

Manual response accuracy

Manual response accuracy was significantly affected by pathway bias (Figure 2C), with a significant main effect of bias $F(2,58) = 33.08$; $P < 0.001$ driven by lower overall accuracy for M stimuli (65.78% for vs. 72.02% for K and 74.96% for P). The main effect of expression was also significant $F(1,29) = 14.49$; $P < 0.001$, as was the main effect of identity $F(1,29) = 121.04$; $P < 0.001$. There effects were driven by the *Expression* *

	Accuracy for angry faces			Accuracy for neutral faces		
	R	*P* (corrected)	Variance explained, %	r	*P* (corrected)	Variance explained, %
K	0.587	$P < 0.01$	34.5	−0.201	$P > 0.4$	4.0
P	0.602	$P < 0.01$	36.2	−0.126	$P > 0.4$	1.6
M	0.582	$P < 0.01$	33.8	−0.070	$P > 0.4$	0.5
	Manual RT for angry faces			Manual RT for neutral faces		
	r	*P* (corrected)	Variance explained, %	r	*P* (corrected)	Variance explained, %
K	−0.479	$P < 0.01$	22.9	0.09	$P > 0.5$	0.8
P	−0.579	$P < 0.01$	33.6	0.276	$P > 0.1$	7.6
M	−0.568	$P < 0.01$	32.3	0.133	$P > 0.5$	1.8

Table. Manual response correlation r-values

Identity interaction, with dramatically lower accuracy for angry female faces (55.03% for angry female faces vs. 76.19% on average for the other conditions, $F(1,29) = 116.99$; $P < 0.001$). As the nonsignificant *Bias * Expression * Identity* interaction suggested and post hoc tests confirmed, the *Expression * Identity* interaction was significant for the three pathway bias conditions (all *P*s < 0.001).

Effects of facial masculinity

To examine the effects of identity cues on facial expression perception in more depth, we used the masculinity ratings we had obtained from the same subjects in the post-test conduct after the experiment proper. Specifically, we used the mean masculinity rating scores for each stimulus to compute correlations with behavioral RT and accuracy for each pathway-biasing condition (Table). For angry faces (Figure 4A,B), facial masculinity positively correlated with response accuracy (K: $r = 0.587$; P: $r = 0.602$; M: $r = 0.582$, all *P*s < 0.01; Figure 4A) and negatively correlated with manual response RT (K: $r = -0.479$; P; $r = -0.579$; M: $r = -0.568$, all *P*s < 0.01; Figure 4B), with a clear bifurcation of the masculinity ratings between male and female faces. However, the saccade latency did not show significant correlations with the masculinity ratings (all r's <0.182, all *P*s > 0.237). For neutral faces (Figure 4C,D), masculinity ratings did not correlate with manual response RT, accuracy, and saccade latency (all $r < 0.170$, all *P*s > 0.27).

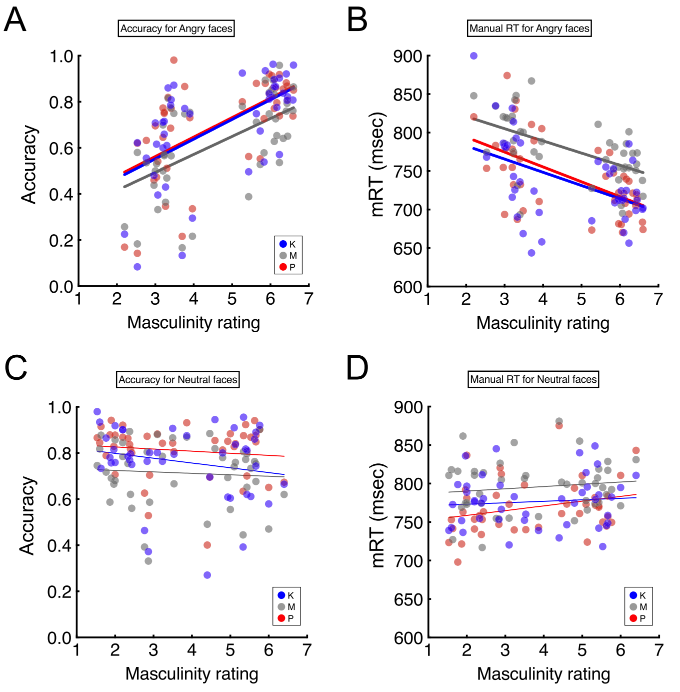

Figure 4. Effects of facial masculinity of manual responses for different emotions of face stimuli. Scatter plots show correlations between facial masculinity rating and *manual response* time for (A) angry faces, (B) manual response *accuracy* for angry faces, (C) manual response *times* for neutral faces, and (D) manual response *accuracy* for neutral faces. The thicker black regression lines indicate statistically significant correlations ($P < 0.05$, corrected for multiple comparisons). Each data point represents the mean for a single stimulus face averaged across all subjects.

Within the male category (both angry and neutral), masculinity ratings significantly correlated with the manual response RT ($r = -0.434$, $P < 0.01$; Figure 5A), but not with response accuracy (all $r < 0.211$, all *P*s > 0.170; Figure 5B) or saccade latency (all $r < 0.185$; all *P*s > 0.229). Within the female category, they significantly correlated with the manual response RT ($r = -0.324$, $P < 0.05$; Figure 5C) for K-biased images and response accuracy ($r = -0.302$, $P < 0.05$; Figure 5D), but not with the saccade latency (all $r < 0.229$, all *P*s > 0.135). The results in Figures 4 and 5 show that manual responses to faces are modulated by compound facial threat cues. Specifically, facial masculinity affects

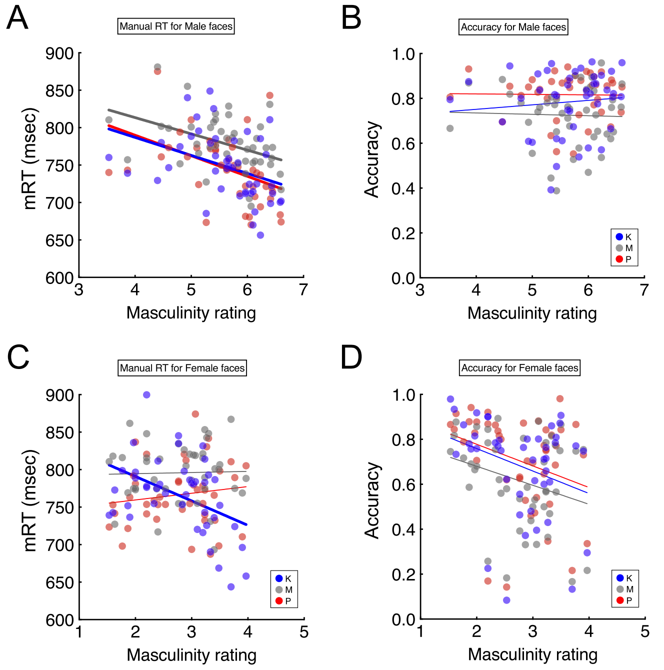

Figure 5. Effects of facial masculinity of manual responses for male and female face stimuli. Scatter plots show correlations between facial masculinity rating and *manual response* time for (A) male faces, (B) manual response *accuracy* for male faces, (C) manual response *times* for female faces, and (D) manual response *accuracy* for female faces. The thicker black regression lines indicate statistically significant correlations ($P < 0.05$, corrected for multiple comparisons). Each data point represents the mean for a single stimulus face averaged across all subjects.

manual response speed and accuracy to faces biased to either K-, P-, or M-pathway, but only for angry faces (Figure 4, top panels), and does not interact with visual pathway biasing. For neutral faces (Figure 4, bottom panels), there were no significant correlations for any of the pathways.

General discussion

The goals of this study were twofold: 1) to test whether complex biological stimuli, human faces, projected to the koniocellular visual pathway, can evoke faster saccadic and manual responses, in comparison to the magnocellular and parvocellular pathways, and whether these responses are modulated by facial threat; and 2) to test whether sex-linked facial identity cues (facial gender/masculinity) modulated perception facial expressive cues differently in the K, M, and P visual pathways. We found that stimuli presented to the K pathway evoked faster saccadic responses, which suggests it is capable of playing a role in rapid targeting for complex stimuli, human faces. However, at least in our task, the saccadic latency did not differ significantly depending on the affective nature of the stimulus, being similar for angry and neutral faces. Thus, we obtained support for our first hypothesis. Our second hypothesis was partially supported, in that we found significant interactions of facial expression and identity cues for manual, but not for saccadic responses. These responses differed by pathway to which the faces were presented. When stimuli were presented to the K pathway, responses were primarily modulated by facial expression, being faster to anger, whereas responses to M-biased faces were modulated by interactions of expression and identity cues. Responses to P-biased faces were not substantially modulated by either expressive or identity cues.

The manual response latencies and accuracies were differentially modulated by facial masculinity and expression cues, and lagged saccadic responses by nearly half a second. We found strong interactions between stable identity cues linked to the expressers' sex (i.e., masculinity), with facial masculinity significantly reducing manual RT to angry male faces. Conversely, more-feminine faces evoked high error rates when presented with an anger expression. This finding is consistent with previous studies finding interactions between stable identity cues, such as race and sex, and facial expressions (Becker, 2017; Hugenberg, 2005; Kveraga et al., 2019; Marsh et al., 2005). Notably, the nature of this interaction differed by the pathway to which these facial cues were presented. Response latencies to stimuli presented to the K pathway were modulated mainly by facial emotion, as responses to angry faces (male and female) were faster than neutral. For the M-biased stimuli, we observed a strong interaction between identity and expressive cues, as responses to angry females and neutral males were slower than those to angry males and neutral females. This supports our previous findings in which different combinations of facial cues (fear with direct or averted eye gaze) engaged the M and P pathway processing depending on the clarity or ambiguity of threat (Cushing et al., 2019; Im et al. 2018; Im et al., 2017). Last, response latencies to the P-biased stimuli were not strongly modulated by either identity or expressive cues, and the interaction, while the pattern was in the predicted direction, did not reach significance. However, response accuracy was significantly modulated by the interaction of facial expressive and identity cues in all three pathways.

Saccadic responses

Our findings show that higher-level stimuli projected to the K pathway can evoke saccades with fairly short latency. There was a significantly greater tendency to generate saccades to K-biased stimuli in the ~200 msec time range than for corresponding P-biased (or M-biased) stimuli, as otherwise the K and P saccadic latency distributions are quite similar. Our findings are in agreement with the results of Hall and Colby (Hall & Colby, 2014; Hall & Colby, 2016) whereby K-biased stimuli were able to evoke activity in the macaque superior colliculus and the animals were able to generate short-latency saccades to such stimuli. The long latencies of sRTs evoked by M-biased stimuli are likely the result of having to resolve a small luminance contrast on rapidly changing (15 Hz) EEG background without the benefit of color opponency signals from either the K or P pathways. Although the superior colliculus is strongly responsive to luminance stimuli, the luminance contrast to generate strong bursts of activity in the SC neurons responsible for generating short-latency saccades needs to be quite high, as saccade generation latency in the SC (Marino et al., 2015) and behaviorally (Kveraga & Hughes, 2005) scales strongly with target luminance.

In our previous experiments using low luminance contrast (<5%) to selectively engage the M pathway with objects (Kveraga et al., 2007), Navon letters (Thomas et al., 2012), scene images (Kveraga, 2014), and faces (Im et al., 2017), we had used a uniform gray background and found that manual response latencies to M-biased stimuli were either shorter than (Kveraga et al., 2007) or similar to (Im et al., 2017), those evoked by P-biased stimuli. However, saccade latencies in experiments employing simple low-luminance contrast stimuli (1° circular targets on black background) were as much as 150 msec longer than sRTs to brighter targets (Kveraga et al., 2002; Kveraga & Hughes, 2005). Therefore, it is not surprising that sRTs to M-biased face stimuli in the present study were much longer, especially given that we also employed a dynamic EEG background (Hall & Colby, 2014; Hall & Colby, 2016), which made stimuli with low luminance contrast more difficult to detect. Although Hall & Colby found sRTs to K targets to be on par with those to luminance targets, they used a much higher luminance contrast for the luminance targets (Hall & Colby, 2016). However, it is important to note that despite the long saccadic latencies to M-biased targets, observers nonetheless were able to do the behavioral task in the M-biased condition quite comparably. Last, our findings show that saccadic RTs overall were not sensitive to facial expression and identity cues.

Effects of stimulus identity on saccadic and manual responses

Face masculinity ratings obtained from the same subjects after the main experiment negatively correlated with RT and positively correlated with response accuracy – but only for manual responses to angry faces. This suggests a strong interaction of stable identity cues (masculinity) and expressive cues (anger). Given that these cues are congruent, both response speed and accuracy were facilitated when the task was to identify angry faces. This is consistent with previous studies reporting interactions of identity and facial expressive cues (Becker, 2017; Im et al., 2017; Kveraga et al., 2019; Marsh et al., 2005; Zebrowitz & Montepare, 2008). The sensitivity of manual responses to *Expression * Identity* interactions, whose primary drivers were lower RT to angry masculine faces and low accuracy to angry feminine faces, shows that sex-linked identity cues strongly affect our responses to threat stimuli. Angry male faces combine congruent threat cues (anger expression and masculine features) and thus signal potential imminent danger, given their greater size, strength, and propensity for aggression. Meanwhile, angry female faces combine incongruent cues of anger and feminine features. This produces strong interference with perceiving anger accurately in female faces, lowering the response accuracy in this condition to the 50%–60% range.

Conclusions

Here, we have shown that high-level stimuli, faces, presented to the K-pathway are able to evoke fast saccadic and manual responses, relative to stimuli presented to P and M pathways. Although the saccadic responses were not strongly modulated by facial expression and identity cues, manual response latencies were sensitive to facial expression, and accuracy patterns showed modulation by both expressive and identity cues and their interaction. We conclude that the koniocellular pathway plays an important role in directing gaze and attention to complex biological stimuli, human faces.

Keywords: magnocellular, parvocellular, koniocellular, threat, expression, identity cues

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